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Population ecology of free-ranging American mink *Mustela vison* in Denmark

PhD thesis

Mette Hammershøj

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Abstract:

This PhD thesis presents the results of various studies of free-ranging American mink *Mustela vison* in Denmark. Stable carbon isotope analyses of teeth and claws from 213 free-ranging mink from two areas in Denmark showed that nearly 80% were escaped farm mink. A genetic analysis of a sub-sample of the same animals by means of microsatellites corroborated this result. The isotope analyses permitted the separation of the mink into three groups; newly escaped mink, 'earlier' escaped mink (having lived in nature for more than ca. two months), and wild mink. The survival of these three groups differed. Once an escaped farm mink had managed to stay alive in nature for more than two months, its chances of survival were as good as for the wild mink. Mink diet consisted primarily of mammals, followed by amphibians, birds and fish. Diet of polecats from the same area is also described. Finally, the thesis gives results from model simulations (including evolution) of the possible effects on the free-ranging population of reducing the number of escapes or completely closing down fur farms in Denmark.

Keywords:	American mink, Mustela vison, Denmark, free-ranging, stable isotopes, microsatellites, survival, diet, individual-based models, genetics, evolution.
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Preface

The present work represents three years of studying the free-ranging mink *Mustela vison* in Denmark in order to obtain the PhD degree at the University of Copenhagen, Denmark.

The thesis consists of a synopsis which reviews the back-ground, summaries and discussions of six scientific articles, and furthermore presents some of the results that were too scant to warrant a separate publication. Four of the scientific articles have been submitted for publication, one has been accepted, and one is present as a manuscript. References quoted in the synopsis are placed at the end of the synopsis. References, not yet published, are quoted by Roman numerals (i.e. Hammershøj & Forchhammer III, Hammershøj et al. VI) and can be identified in the table of contents.

This PhD was financed as a joint project between the Danish National Environmental Research Institute (NERI) and the Danish Research Training Council with supervisors from NERI and University of Copenhagen. Additional financial support was gratefully received from the Danish Forest and Nature Agency, the Danish Furbreeders Association and the Danish Animal Welfare Society.

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1 Synopsis

1.1 Background and aims

The American mink *Mustela vison* is not a native species in Denmark. It was imported to Danish mink fur farms in the early 1930s. Since then, an unknown number of mink have escaped from these farms. According to the Danish Game Bag Record the annual mink bag has increased from less than 1,000 in the 1970s to 7-8,000 in the past five years. It is likely that this increase reflects an increase in population size of free-ranging mink.

Essential knowledge about the fundamental biology and population ecology of free-ranging mink in Denmark is lacking. Increasing concern has arisen about the damage that free-ranging mink may cause the native fauna – both in relation to prey populations and to populations of other mustelids / predators, especially polecats *M. putorius* and otters *Lutra lutra*.

Numerous studies show that free-ranging mink represent a potential problem in nature management, either as competitors to indigenous mustelid species, or as predators in relation to a number of wild bird and mammal species (e.g. Lodé 1993; Clode & Macdonald 1995; Kilpi 1995; Halliwell & Macdonald 1996; Craik 1997; Barreto et al. 1998; Riley et al. 1998; Ferreras & MacDonald 1999; Nordström et al. 2003). Thus, control of free-ranging populations of American mink is an important nature conservation issue in most European countries. In Denmark, however, the situation is somewhat different from most other countries in that fur farming is still a thriving business. Denmark has by far the highest concentration of mink fur farms in the world (European Commission 2001) with 2,392 operating farms holding 2,2 million breeding females and with an annual production of 11 million pelts in 2000 (Statistical Yearbook 2001).

As a basis for an evaluation of possible problems regarding free-ranging mink in Denmark, we examined the distribution of mink bagged by hunters in Danish nature in 1996 / 97. We found that mink were widely distributed across Denmark (Hammershøj & Asferg 1999).

The geographical distribution of bagged mink closely reflected the concentration of mink fur farms as the highest number of mink were taken in areas that also had a high concentration of mink farms (Hammershøj & Asferg 1999). These results indicate that mink farms and their immediate surroundings might act as source ”habitats” and that areas far from mink farms might act as sink habitats (cf. Wiens 1990).

The observed increase in the number of free-ranging mink in Denmark may indicate an increase in the number of mink escaping from farms and / or an increase in the ”natural” reproduction in the population of free-ranging mink.

Regardless of the reason for the increase, the American mink, being an alien, invasive species, is generally unwanted in Denmark. As opposed to most Danish game species which are protected in their breeding season, mink can be hunted year-round. According to government order LBK no. 818 of 11.12.1987, escaped fur animals that are not recaptured within two months are considered game, and are thus included in government order BEK no. 801 of 22.09.1999, which states that escaped fur animals that are considered game can be hunted/controlled all year, i.e. they are not protected in the breeding season.

However, the best choice of future management strategies aiming to reduce or eliminate the population of free-ranging mink will depend on the reason for the increase. Consequently, it is crucial to be able to determine the origin of free-ranging mink, i.e. whether they are mainly escapees from fur farms or members of a truly ”wild” population.

The purpose of this Ph.D.-project was to provide basic knowledge about the biology and population ecology of free-ranging mink in Denmark, including interactions between the species and its surroundings, and specifically to answer the following questions:

- How large a proportion of the free-ranging mink population consists of escaped farm animals?

- Can the free-ranging mink sustain viable populations via reproduction in nature or is it dependent on a continuous supply of escaped farm animals?

- What are the survival rates and how is the state of health of free-ranging mink?

- What effects do free-ranging mink have on prey populations and on native predators?

- Conclusions and management perspectives

The Danish Forest and Nature Agency carried out a three-year mink control scheme in two areas, the Thy State Forest District in north-western Jutland and the State Forest District on Bornholm, a Danish island in the Baltic Sea. Animals were trapped in instant-kill traps. All animals from Thy were caught in the winter half-years (September-March) of 1998-2000. Mink from the island of Bornholm were caught year-round in 1999-2001. All trapped animals were frozen and handed over to NERI, and most of the PhD project was based on data derived from these animals (mink and polecats). For some of the animals complete data were not received and for other animals only some examinations could be performed. Therefore, the number of individuals in the various examinations varies.

1.2 Wild mink or escaped farm mink?

Danish farm mink are fed a specific diet differing from a natural diet. Farm feed has a relatively high content of marine fish and slaughter offal from pigs compared to a natural diet for (inland) mink. The diet composition is reflected in different tissues of the animals. Thus, a number of different methods could possibly be used to distinguish between escaped farm mink and wild mink.

In recent years, several studies have used stable isotope analyses to distinguish between populations of different animal species feeding on marine or terrestrially based diets (e.g. Kelly 2000). For instance, Angerbjörn et al. (1994) found significant differences in carbon isotopic signatures of coastal vs. inland Arctic foxes *Alopex lagopus*.

We tested the possibilities of distinguishing between escaped farm mink and wild mink by stable carbon isotope ratios and lipid profile analyses and performed a feeding experiment in order to determine persistence of carbon isotope ratios in claws and teeth after a change of diet (Asferg et al. I).

Using lipid profile analyses it was possible to distinguish between escaped and wild mink, though differences only persisted for a few weeks after a change to a natural diet. In contrast, carbon signatures in permanent teeth were considered to be stable once the teeth were fully developed. By combining the carbon signatures in claws with the signatures in teeth for each animal, the stable carbon isotope analysis permitted the separation of free-ranging mink into three groups; 1) mink that had been raised and probably born in nature, 2) mink that were born in a farm and had been free-ranging for more than approx. two months, and 3) mink that were born in a farm and recaptured less than approx. two months after the escape (Asferg et al. I).

Analysis of stable carbon isotopes was then performed on teeth and claws of the free-ranging mink (Hammershøj et al. II). A classification based on empirical data (n=213) resulted in three groups; 47% were ***newly escaped farm mink*** and another 31% ***"earlier" escaped mink*** had been born in farms and lived in nature for more than approx. two months. The remaining 21% may or may not have been born in nature, but they had been free-ranging for more than a year and were thus considered ***wild mink***. A possible source of error to this result would be mink living and feeding in coastal habitat, or inland mink feeding on anadromous fish. However, no differences were found in carbon signatures between mink caught in inland as opposed to coastal habitat, indicating that the mink did not feed on marine fish to any great extent. These results were further supported by a diet analysis performed on the same individuals, since no marine fish and only a very few anadromous fish (in less than 2% of 211 mink) were found in the gastrointestinal tracts (Hammershøj et al. IV).

The results were supported by a genetic analysis by means of microsatellites that was performed on a subsample of the trapped mink (86 individuals) and on 70 farm mink (Hammershøj et al. II). In agreement with the carbon isotope results, there was strong genetic evidence for a high percentage of escaped farm mink in the free-ranging population (86%). In 93% of the cases, both carbon isotope and genetic analyses classified a given individual to the same category.

The proportion of farm mink in the free-ranging populations was higher in Thy than in Bornholm. These regional differences suggest that in order to make realistic management plans for free-ranging mink, populations from several additional areas in Denmark should be sampled. It is of particular priority to analyse mink from areas with no or few fur farms.

Both stable isotope and microsatellite analyses can be used to distinguish between farm and wild mink, but whereas microsatellites can only reveal whether a given mink originated from a farm or not, carbon isotopes offers more detail on the period of time a farm mink has been living in natural habitats. Furthermore, in order to be able to use microsatellites in the whole country, samples of every farm mink colour strain have to be analysed which would be a daunting task. In contrast, carbon isotope analyses can be used nation-wide with the possible exception of coastal habitats.

1.3 Survival rates and state of health of free-ranging mink

We investigated the survival of the three groups of free-ranging Danish mink, i.e. newly escaped mink, "earlier" escaped mink (having been free-ranging for more than approx. two months), and wild mink (Hammershøj & Forchhammer III). Individuals were aged, counting growth lines in longitudinal sections of calcified canines, and survival rates were calculated. The survival rate of newly escaped mink was significantly lower than that of both wild mink and "earlier" escaped mink, whereas the survival rates of the two latter did not differ significantly. A comparison with published data on a Swedish feral population (Gerell 1975) and a native US population (Askins & Chapman 1984) showed no significant differences in survival rates between these and Danish wild and "earlier" escaped mink. Both populations did, however, differ significantly from the newly escaped mink (Hammershøj & Forchhammer III).

The results show that once an escaped farm mink has managed to stay alive in nature for more than two months, its chances of survival are as high as for the wild mink, suggesting a quick adaptation to natural conditions. This was further supported by the diet study, in which no differences in diet were found between the three groups of mink (Hammershøj et al. IV). Body condition, in terms of weight and length of the mink (Clode et al. 1995), was compared for the three groups of mink, but no clear pattern emerged (unpubl. data).

The free-ranging mink were necropsied by veterinarians from the Danish Veterinary Institute using a routine necropsy procedure. The animals were checked for antibodies to Aleutian disease virus (ADV) and for distemper virus antigens, and for presence of Salmonella, Campylobacter and parasites.

Ten (4.3%) of 223 examined mink tested positive for antibodies to ADV. A similar proportion was found in Iceland, where 14 (3.6%) of 394 feral mink were positive for ADV antibodies (Skírnisson et al. 1990). Eight of the Danish positive mink were from the island of

Bornholm, representing a third of the examined mink from the island, and six of them were wild mink (Hammershøj et al. II). This could present a possible problem for mink farmers if virus is spread to the farms via free-ranging mink. Furthermore, ADV could infect other mustelids. Yamaguchi & Macdonald (2001) found Aleutian disease antibodies in 14 (51.9%) of 27 mink in southern England. They speculated that the occurrence of this viral disease in a feral American mink population could threaten populations of at least two protected mustelids, the otter and the polecat. In Spain, Mañas et al. (2001) found antibodies to Aleutian disease in 3 of 9 European mink *M. lutreola*, and ADV DNA was detected by polymerase chain reaction in whole cell DNA from 4 of 7 carcasses; two American mink, one European mink, and one otter. A serological survey of 446 ferrets *M. putorius furo* owned by members of a British ferret club revealed an incidence of 8.5% ADV seropositive animals (Welchman et al. 1993). One of the possible sources of ADV were stray ferrets taken in, which were thought to have become infected through contact with feral mink. Thus, presence of ADV in free-ranging mink could present a serious problem to native carnivores belonging to Mustelidae.

However, the Aleutian disease virus itself could not be detected in any of a number of Danish mustelids tested positive for antibodies in a later study (Anne Sofie Hammer, pers. comm.). ADV is still present in Danish fur farms though (in 1.7% of 2047 tested farms, Willadsen 2003), and as long as this is the case and farm mink escape from the farms, there is a risk of mink infecting other wildlife.

Distemper virus antigens was tested for in mink from Thy (n=95), but all tests proved negative for the virus. Distemper virus infection is a potentially fatal disease in mink, but the susceptibility varies and some infected animals may raise protective antibodies and be protected against infection for life (Hans Henrik Dietz, pers. comm.). Other carnivore species can also be infected, and one example is the black-footed ferret *M. nigripes* which is especially susceptible to distemper virus infection (Williams et al. 1988). Thus, it cannot be ruled out that distemper had been present in the free-ranging mink population but the fact that not even early stages of distemper were found makes this unlikely.

It has been speculated that distemper virus in mink could be responsible for outbreaks of Phocine distemper virus (PDV), a closely related morbillivirus, in seals (Örvell et al. 1990). The opposite situation is definitely believed to have occurred, in that the PDV causing an epidemic among harbour seals *Phoca vitulina* in 1988 was transmitted from diseased seals to terrestrial carnivores causing distemper epizootics among Danish farm mink in 1989 (Blixenkrone-Møller et al. 1992). A new seal PDV epidemic occurred in Danish waters in 2002 (Dietz et al. 2003). The method used in the present study for detecting distemper virus antigens would also show PDV, or any other morbilivirus, if present, but none were found (unpubl. data). Any theory of mink causing the recent PDV outbreak can thus not be corroborated from our data.

Salmonella was not detected in any of 223 examined mink, nor was Campylobacter spp. (n=116, all from Thy). However, it should be born in mind that the material had been frozen and that e.g. Campylobacter spp. generally does not survive freezing (Hans Henrik Dietz, pers. comm.). Only Thy mink (n=96) were examined for parasites. Oocysts of Coccidia were found in 7 (7.3%) mink, and nematode eggs were found in 3 (3.1%). This seems a rather small number compared to e.g. a study in Belorussian Polesie, in which the overall rate of infection of 50 American mink by helminths was 78%, nematodes being the most frequently detected parasite (Shimalov & Shimalov 2001). In a Spanish study, 41% of 112 American mink were infected by helminths (Torres et al. 2003). However, in our study, only faecal examination was performed and the material was often in a rather decomposed state adding to the decomposition of parasites and parasite eggs caused by prolonged freezing and repeated thawing procedures (Hans Henrik Dietz, pers. comm.). Lungworms (*Crenosoma* spp.) were found in all of 40 examined polecats from Thy, but in none of the mink (unpubl. data).

Regarding the above mentioned diseases, the health status of free-ranging mink in Denmark was found to be generally good.

1.4 Viable populations via reproduction in nature or because of continuous supply of farm mink?

There is little doubt that mink reproduce under natural conditions in Denmark, but we do not know to what extent they do so. In order to establish this, we examined uteri (placental scars (Madsen & Rasmussen 1985; Elmeros & Madsen 1999)) from the trapped free-ranging mink females and also from 120 farmed mink with known breeding history to "calibrate" the method. Mink only breed once a year, and unfortunately, placental scars disappear very quickly in mink. Examinations of the farm uteri showed that the number of placental scars only gave a reliable estimate of number of cubs in farm mink killed in summer (unpubl. results). In farm mink killed in November, there was a significant disagreement between number of placental scars visible and number of cubs born, and in some cases, no placental scars were visible despite the female having given birth to several cubs in April / May (unpubl. results).

Since the vast majority of our free-ranging mink had been caught in the winter half-year (September through March), the results from the examination of placental scars were rather poor. Of 47 adult females, 9 had one or more placental scars, showing that they had indeed given birth. This must be considered an absolute minimum estimate of the proportion of mink having reproduced in nature.

Of the 9 mink with placental scars, 8 were born in farms and may thus, have been impregnated and possibly have given birth in farms. Only one female (from the island of Bornholm) had scars and had been living in the wild for more than a year. One female had 9 foetuses in the uterus, but specific details on the female were not available.

The fact that 60% of the wild mink (n=45), i.e. mink having lived in nature for at least a year, were less than one year of age (Hammershøj

& Forchhammer III), strongly suggests that mink do breed in the wild, even though some of the offspring may have been conceived in farms.

It is still uncertain, however, whether the mink population can survive in nature without a continuous supply of escapees from fur farms. Afterall, 79% of the free-ranging mink in our study areas were escaped farm mink (Hammershøj et al. II).

In an attempt to shed some light on this question, we developed an individual-based patch occupancy model framework for diploid organisms that reproduce sexually (Travis et al. V). Patch occupancy models are widely used within ecology to study spatial processes (e.g. Dytham 1994, 1995, Hill & Caswell 1999, Travis 2003). In its simplest form, a patch occupancy model is spatially implicit, and the colonisation of a patch is thus equally like to occur from any other patch. No explicit concern is taken regarding exactly where one patch is situated relative to another. A patch is either occupied or unoccupied. Levins' (1969) meta-population model was the first spatially implicit patch occupancy model. In a spatially explicit patch occupancy model, the spatial relationship between patches is considered explicitly.

In our model, the landscape is represented as a number of cells in a grid, a cellular lattice/automata. Each cell can hold one or no individuals. Every individual on the lattice is given a probability of being the maternal parent of an offspring, and the offspring disperses to one of the eight cells neighbouring its natal patch. The proposed model framework can readily incorporate different genetic processes including mutation, recombination and epistasis. We showed that the model can be used to investigate the evolutionary dynamics of an invasive species. Artificial selection or adaptation to captive environments typically results in reduced fitness under natural conditions (Tufto 2001, Gilligan and Frankham 2003, and references therein). In our model, an individual's genotype determines the probability that it successfully establishes at a suitable site. If the introduced individuals are genetically well-adapted to the wild conditions, the number of mink in the wild is always larger when there are more introductions. However, if the introduced individuals are genetically poorly adapted to natural conditions, as might be expected for farm mink, this is often not the case. Under these conditions, the most rapid invasion occurs for an intermediate number of introductions. When the number of introductions is high, genetic adaptation to local conditions is dramatically slowed and in some cases a genetically well-adapted population never establishes. This is not an unknown phenomenon, and has been described in connection with expanding populations, in which gene flow from the centre of a species' range can stymie adaptation at the periphery and prevent the range from expanding outward (e.g. Kirkpatrick and Barton 1997).

In order to describe the spatial population dynamics of the Danish mink population in more detail, we further developed our model, and allowed for each cell to hold several different individuals (Hammershøj et al. VI). This model was based on a real landscape (Denmark) and predicted the distribution of free-ranging mink from geographic locations of Danish fur farms, the number of breeding mink kept per farm, and a range of parameters regarding escape, reproduction, mortality, and dispersal. Different habitat types can readily be incorporated in the model framework, but we simply differentiated between water and land. The model was validated against real data on distribution of free-ranging mink bagged by hunters (Hammershøj & Asferg 1999), and there was a highly significant correspondence between the model output and the real data.

We then incorporated evolution, i.e. genetic properties, in the model, and allowed for variation of some of the parameters, e.g. the number of mink escaping from the farms, whether or not escapes would become limited or completely stopped after a number of years, how many females were allowed to breed per km^2, the proportion of well-adapted alleles in escaping mink, how important being well-adapted was for survival, and the magnitude of mutation. Only one parameter was varied at a time, and the model was run for 100 model years. Within most tested parameter ranges, limiting or completely stopping escapes from farms from year 25 onwards, always made mink in the wild become better adapted to natural conditions and thus, reach higher population sizes, quicker than if escapes were to occur at the same rate. However, one parameter, describing the relative benefits on fitness of beneficial alleles, had a big effect on the model results. The results suggested that if the fitness benefit is relatively low, reducing or stopping escapes from farms is likely to reduce the population in the wild, while if the benefit is relatively large, closing farms may not have the desired effect. Thus, the results from our model do not support the hypothesis that fur farms today act as sources and areas away from farms as sinks (cf. Wiens 1990). Quite the opposite can be the case, in that the continuous escapes from fur farms may actually keep mink in nature at a genetically less well-adapted stage and thus, at lower population sizes, than would be the case if there were no further escapes from fur farms. Given that the model predictions differ so much depending upon the parameterisation, the question of whether viable mink populations can persist via reproduction in nature or is dependent on a continuous supply of farm mink, can not be answered fully with the present knowledge of mink genetics.

1.5 Effects of free-ranging mink on prey populations and native predators

The relative importance of trophic interactions was examined via food choice analyses of stomach/intestine contents of the collected free-ranging mink from Thy and Bornholm (Hammershøj et al. IV). The majority of the animals were caught from September through March, thus, summer diet is insufficiently represented. A diet analysis of the stomach/intestine contents of trap killed polecats from Thy was also performed to evaluate a possible (seasonal) competition for food between mink and polecat (Hammershøj et al. IV). Mink is the only mustelid present on Bornholm.

Sympatric mink (from Thy) preyed mostly on mammals (55% of the mink), followed by amphibians (36%), birds (35%) and fish (30%), while polecat preyed mostly on amphibians (87%) and mammals

(34%) and occasionally on birds (9%) and fish (6%). Allopatric mink (from Bornholm) preyed mostly on birds (50%), followed by mammals (42%), fish (25%) and amphibians (4%). With the possible exception of some amphibians, no endangered species were found in their diet. No significant difference in food choice was found between newly escaped, "earlier" escaped, and wild mink (Hammershøj et al. IV). Despite a fairly large food niche overlap between mink and polecat, the two species seem to coexist without major negative effects on either species, although more data is needed.

Mink diet was also compared to otter diet in freshwater localities in Denmark described in literature (Hansen & Jacobsen 1992). As opposed to our study, the otter study was performed on animals from all seasons. However, the otter diet was clearly dominated by fish and, to a lesser extent, amphibians through-out the year, and we concluded that mink and otter do not seem to compete for food to any great extent, with the possible exception of winter feeding on frogs (Hammershøj et al. IV). Thus, the concern that mink in general might have a detrimental effect on its prey species and other mustelids in terms of food competition in Denmark may be unjustified. It cannot be ruled out, however, that mink may locally have a negative effect on some specific prey species, and clearly, more data is needed on e.g. prey abundance and mink diet in spring, i.e. the breeding season of birds, in order to make any definite statements.

In order to establish how mink and polecats react to the presence of each other, we carried out a radio-telemetry study in Kolindsund, Eastern Jutland. Unfortunately, we were only able to fit radio-transmitters onto three mink, two of which disappeared within the first month. With only one radio-tagged mink, we decided to concentrate on polecats, of which we had four males fitted with radio-transmitters (with active/inactive pulse) for 32-100 days. This part of the study was carried out as part of a Masters' thesis (Thomsen 2002).

The few data that we did get on two mink revealed that mink and polecats shared the same habitats to some extent, and even used the same den on one occasion, although not at the same time. Some of the mink and polecats were caught in the same traps. An untagged mink was once observed during the daytime, when it investigated, from the outside, a burrow in which a tagged polecat was sleeping. The polecat became active for a very short period, but soon returned to a stable inactive phase (pers. obs.).

Some data was gathered on mink movements in the area (42 radio locations of two female mink during less than two months). The mink were never observed further than 20 meters away from a canal that was running through the area (unpubl. data). This pattern is typical in mink that normally have linear home ranges along streams, lake sides or coast lines (Gerell 1970, Birks & Linn 1982). In contrast, the polecats in the Kolindsund area had two-dimensional home ranges, some of them including three canals (Thomsen 2002). These findings are in accordance with other studies on mink and polecat (e.g. Gerell 1970, Birks & Linn 1982, Blandford 1987, Lodé 1993). Thus, our observations suggest that mink and polecat may avoid each other, but are well able to coexist in the same habitats.

Another possible negative effect of mink on other species could be as a transmitter of infectious diseases. Diseases transmitted from alien species, especially feral domestic animals, has caused severe losses of native carnivores in the past (Macdonald 1996). In the present study, we did not find evidence of this (Chapter 1.3), but the risk should not be dismissed.

Hybridisation between American mink and native mustelids has also been mentioned as a possible problem. Hybridisation does not necessarily mean that a parental taxon is genetically threatened (Simberloff 1996). Hybridisation's can fail to produce offspring – as do those between European mink, a species that does not exist (and never has) in Denmark, and American mink (references in Rozhnov 1993) and between American mink and ferrets (Chang 1968). Nevertheless, hybridisation can threaten a species by preventing it from reproducing. For instance, American mink become sexually active earlier than European mink and are larger. Thus, American mink males mate with European mink females as the latter come into oestrus. These impregnated females then repel other males, reabsorb embryos and leave no offspring that year. American mink reproduction and recruitment proceed normally (Simberloff 1996). However, hybridisation under natural conditions between mustelids has only been described on a few occasions (references in Rozhnov 1993; Davison et al. 1999), none of which included American mink, and the problem is therefore considered hypothetical.

1.6 Conclusions and management perspectives

Our studies have shown that a major part of the free-ranging mink population in Denmark consists of fur farm escapees. A large proportion of the newly escaped farm mink die within the first two months of escape. However, the ones that do survive, soon become behaviourally adapted to living under natural conditions. The free-ranging mink were found generally healthy. We did not detect any major negative effects of mink on its prey species nor on native mustelids, i.e. polecats and otters, although more studies, including summer diet and assessment of prey abundance, are needed.

We were not able to determine to what degree free-ranging mink reproduce in nature, but other data strongly suggests that mink do breed in the wild. It is still uncertain whether the mink population can survive in nature without a continuous supply of escapees from fur farms. Our general model on invasive species suggested that the continuous supply of genetically poorly adapted farm mink may, somewhat counter-intuitively, prevent the establishment of a truly feral population, but our more detailed mink model lent only some support to this. One of our 'best guess' parameters proved to have a major influence on the model results, and we were therefore unable to make any firm conclusions.

Most researchers working with invasive species agree that the most effective way to deal with invasive introduced species, is to discover them early and attempt to eradicate or at least contain them before they spread (e.g. Williamson & Brown 1986, Myers et al. 2000, Conover 2001, Allendorf & Lundquist 2003, Simberloff 2003). However, in the case of widespread and/or long-established invasions, and invasive species with high dispersal abilities which will continue to re-establish populations, eradication seems not to be a management option (Usher 1986).

A number of methods have been used/suggested to control unwanted mustelids, e.g. hunting and trapping (Conover 2001), fertility control (Tuyttens & Macdonald 1998), bounty hunting (Hersteinsson 1999), hunting with dogs (Hersteinsson 1999, White et al. 2003), and poisoning of hen eggs (Dilks & Lawrence 2000, Spurr 2000), but none have proved effective in eradicating mink on a national scale, once the species has become established. In Iceland, the first law which stated categorically that mink should be eradicated, was passed by the Althing (parliament) in 1949 (Hersteinsson 1999). With the new law, each local authority was made responsible for employing hunters to search for and kill mink within the boundaries of the community. Despite this, feral populations are still present all over Iceland in suitable habitats (Hersteinsson 1999).

As an alternative to complete eradication, one can attempt to locally eradicate mink and subsequently keep them out of an area, but this requires a constant hunting/trapping effort, which is very time consuming and thus extremely costly (Moore et al. 2000). An (unsuccessful) eradication campaign of the Ministry of Agriculture in Britain in a 5-year trapping programme cost £105,000 between 1965 and 1970 (Dunstone 1993). The cost of the campaign (excluding associated research costs) has been estimated, at 1990 costs, at £552,000 (Baker 1990). The strategy of eradicating mink is probably only warranted in particularly sensitive areas holding large populations of ground-nesting birds, e.g. nature reserves for breeding birds.

In wildlife conservation, there is always a balance between on the one hand, controlling an invasive species and on the other, minimising disturbance and unintentional deaths of non-target species during the control campaign (Usher 1986, Zavaleta et al. 2001). Although an invasive species may be harmful to the natural environment in which it occurs, the adverse effects on the environment of control measures should be considered carefully (Usher 1986, Zavaleta et al. 2001). In the control campaign, carried out in Thy by the Danish Forest and Nature Agency, 209 mink were killed during the three-year control scheme, but there were also unintentional deaths of 58 polecats, 34 stoats *M. erminea*, 10 weasels *M. nivalis*, and 4 stone martens *Martes foina*, as well as a number of rodents and birds (unpubl. data). The effect on the populations of these species is unknown.

The high proportion of escaped farm mink in the Danish nature strongly suggests that fur farms have not been adequately secured against escapes of mink in the past. In a recent government order (no. 610 of July 19. 2002) restrictions were put on mink farmers to more effectively keep mink from escaping. Ensuring that no more farm mink escape from fur farms could result in three different outcomes; 1) the free-ranging population will crash and leave only small, isolated populations that may or may not go extinct, i.e. the farms act as sources and nature as sink, 2) the free-ranging population might crash at first but will then "grow" back to the present level, i.e. the population size is at its carrying capacity, farm mink or not, or 3) a truly feral population genetically adapted to the Danish environment will become established at a new equilibrium.

According to the Danish Game Bag Record, the annual mink bag has been stable around 7,000-8,000 mink in the previous five years. This could suggest that the free-ranging mink population has reached its carrying capacity in Denmark.

Our model (Hammershøj et al. VI) results do not provide any definite answers on which of the above mentioned three outcomes is more likely or on how to get rid of free-ranging mink in Denmark. The only parameter resulting in the extinction of mink in nature is one that cannot be controlled, namely the relative benefit on fitness of well-adapted alleles. With more and better data on mink, we will be able to improve our model, and we hope our results will motivate future studies that can help reduce the uncertainty associated with those model parameters about which we have the least information.

In my opinion, several things speak against allowing the general use of killing traps in an attempt to eradicate mink in Denmark. First, all mink eradication campaigns so far have been unsuccessful whenever they have been performed on a national scale. Second, the use of killing traps often results in unintentional deaths of non-target species. Third, we have not been able to show any major negative effects of mink on neither prey species nor other mustelids in Denmark, although more studies are needed. Fourth, our model results suggest that limiting or completely stopping further escapes from fur farms, may result in the establishment of a self-sustainable feral mink population.

However, nothing as such, speaks against allowing the use of killing traps to control mink in areas (typically islands) where other species, otherwise at risk of being caught in the traps, are not present. Also, in particularly sensitive areas (cf. above), in which protected species are at risk of being eradicated by mink, allowing the use of killing traps by skilled trappers may be considered.

Certainly, in areas (e.g. islands) where there are no fur farms and no records of free-ranging mink, permissions to establish new fur farms should not be given.

Furthermore, in my opinion, despite the lack of "hard" evidence that mink breed in the wild in Denmark, it should be carefully considered giving the mink the same rights as other game, namely protecting the animals in their breeding season.

Without a common strategy based on detailed population biological knowledge, there may not be any major effects of controlling mink. Besides improving our model, obtaining better data on reproduction will also enable us to build matrix population models and perform elasticity analyses (Caswell 2001), that can help identify critical life-history stages during which control will be most successful (Benton & Grant 1999, Caswell 2000). Detailed population biological research is thus likely to aid in fine-tuning control, and it may even lead to new control methods (Simberloff 2003).

As yet, there are no management plans for mink in Denmark. The work presented in this thesis will hopefully be a first step in helping wildlife managers make informed decisions about strategies for the management of free-ranging mink in Denmark.

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Article I, accepted with revision, Mammalian Biology.

Stable carbon isotopes can separate wild American mink from fur farm escapees

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Abstract

Control of free-ranging populations of American mink is a nature conservation issue in most European countries. In Denmark, however, because of the many fur farms, selection of the most adequate strategy to control or reduce the free-ranging mink population will depend on the main source of recruitment to the population. If most free-ranging animals originate from fur farms, efforts should concentrate on measures to prevent animals from escaping from the farms. If most animals are recruited through ”natural” reproduction in nature, a completely different strategy has to be adopted. We tested the possibilities of distinguishing between escaped farm mink and wild mink by stable carbon isotope ratios and lipid profile analyses and we performed a feeding experiment in order to determine persistance of carbon isotope ratios after a change of diet.

Lipid profile analyses could distinguish between escaped and wild mink, but only for a few months after a change to a natural diet, whereas carbon signatures in permanent teeth are considered to be stable once the teeth are fully developed. By combining the carbon signatures in claws with the signatures in teeth for each animal, the stable carbon isotope analysis permitted the separation of free-ranging mink into three groups; 1) mink that had been raised and probably born in nature, 2) mink that were born in a farm and had been free-ranging for more than ca. two months, and 3) mink that were born in a farm and recaptured less than ca. two months after the escape.

Key words: *Mustela vison*, carbon isotopes, feeding experiment, lipid profile, Denmark

Article II, submitted to Journal for Nature Conservation

Danish free-ranging mink populations consist mainly of farm animals: evidence from microsatellite and stable isotope analyses

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Abstract

Two methods were used to separate free-ranging mink *Mustela vison* into wild mink and escaped farm mink. Analysis of stable carbon isotopes was performed on teeth and claws of 226 free-ranging mink from two areas in Denmark. A classification based on empirical data resulted in three groups (n=213); 47% were newly escaped farm mink and another 31% had been born in farms and lived in nature for more than ca. two months. The remaining 21% may or may not have been born in nature, but they had been free-ranging for more than a year and were thus considered wild. A genetic analysis by means of microsatellites was performed on a subsample of the trapped mink (86 individuals) and on 70 farm mink, in order to assess the proportion of escaped farm mink in the free-ranging population. Strong genetic evidence for a high percentage of escaped farm mink in the free-ranging population (86%) was found, in agreement with the carbon isotope results. Both methods can be used to distinguish between farm and wild mink, but whereas microsatellites can only say whether a given mink originated from a farm or not, carbon isotopes can give some more detail on the period of time that a farm mink has been living in natural habitats. The high proportion of escaped farm mink in the Danish nature could have serious implications for the preservation of other vulnerable species and should be carefully considered when designing conservation strategies.

Key words: carbon isotopes, farm mink, microsatellite DNA, Mustela vison, wild mink

Running title: Composition of the Danish free-ranging mink populations

Article III, submitted to Wildlife Biology.

Survival rates of free-ranging farm mink suggest quick behavioural adaptation to natural conditions.

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Abstract
We investigated the survival of three groups of Danish free-ranging mink, i.e. newly escaped mink, "earlier" escaped mink (having been free-ranging for more than ca. two months), and wild mink. Individuals were aged, counting growth lines in cross sections of calcified canines, and survival rates (across cohorts) were calculated. In Denmark, the survival rate of newly escaped mink was significantly different to both wild mink and "earlier" escaped mink, whereas the survival rates of the two latter did not differ significantly. A comparison with published data on a Swedish feral population and a native US population showed no significant differences in survival rates between these and the Danish wild and "earlier" escaped mink. Both populations did, however, differ significantly from the newly escaped mink. These results show that once an escaped farm mink has managed to stay alive in nature for more than two months, its chances of survival are as good as for the wild mink, suggesting a quick behavioural adaptation to natural conditions.

Key words: farm mink, incremental lines, Mustela vison, survival curves, wild mink

Article IV, submitted to Wildlife Biology

Diet of free-ranging American mink in Denmark and competition with polecat and otter

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Abstract

Stomach and intestine contents of 211 American mink from two areas (Thy and Bornholm) in Denmark were analysed. The stomach contents of 47 polecats from Thy were also analysed. Sympatric mink (from Thy) preyed mostly on mammals (55% of the mink), followed by amphibians (36%), birds (35%) and fish (30%), and polecat preyed mostly on amphibians (87%) and mammals (34%) and occasionally on birds (9%) and fish (6%). Allopatric mink (from Bornholm) preyed mostly on birds (50%), followed by mammals (42%), fish (25%) and amphibians (4%). Apart from some amphibians, no endangered species were found in their diet. Despite a fairly large food niche overlap between mink and polecat, the two species seem to coexist without major negative effects on either species, although more data is needed. Mink diet was also compared to otter diet in Denmark described in literature, and we conclude that mink and otter do not seem to compete for food to any great extent, with the possible exception of winter feeding on frogs. Thus, the concern that mink in general might have a detrimental effect on its prey species and other mustelids in Denmark seems unjustified. It cannot be ruled out, however, that mink may locally have a negative effect on some specific prey species.

Keywords: *Mustela vison*, stomach contents, dietary overlap, *M. putorius, Lutra lutra*, Mustelidae

Running title: Diet of *Mustela vison* and food competition

Article V, submitted to Evolutionary Ecology Research

A spatially-explicit model framework for sexually reproducing organisms.

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Abstract

Patch-occupancy models are widely used within ecology to study spatial processes. Here, we extend this well-established framework by developing a patch occupancy model for diploid organisms that reproduce sexually. The proposed framework can readily incorporate different genetic processes including mutation, recombination and epistasis. By way of example, we show how the model can be used to investigate the evolutionary dynamics of an invasive species. In this example, an individual's genotype determines the probability that it successfully establishes at a suitable site. If the introduced individuals are well-adapted to the wild conditions, then the number of escapees is always larger when there are more introductions. However, when the introduced individuals are relatively poorly adapted to the natural conditions this is often not the case. Under these conditions, the most rapid invasion occurs for an intermediate number of introductions. When the number of introductions is high, adaptation to local conditions is dramatically slowed and in some cases a well-adapted population never establishes. We believe that the framework described in this paper can be a powerful tool for biologists interested in the genetics and evolution of spatially structured populations.

Keywords: genetics; simulation; introduced species; invasion; lattice model; patch occupancy

Running title: A patch-occupancy model for sexual organisms

Article VI, manuscript prepared for Oikos

Closing down fur farms may result in the establishment of a feral mink population in Denmark

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Abstract

In this paper, we present an individual-based cellular lattice model, which is based on a real landscape (Denmark). The model predicts the distribution of free-ranging mink from geographic locations of fur farms, the number of breeding mink kept per farm, and a range of parameters regarding escape, reproduction, mortality, and dispersal. The model was validated against real data on distribution of free-ranging mink bagged by hunters, and we obtained reasonable correspondence between the model results and the hunting data. When evolution was incorporated in the model, the results of the model showed that the degree of adaptation within the free-ranging mink population is likely to vary spatially, with lower adaptation in areas where farm mink density is highest (due to the greater number of escaping mink). We used the model to explore the potential consequences of closing mink farms, or limiting escapes from them, on the evolutionary ecology of the free-ranging population and found that depending upon the paramaterisation of the evolutionary processes, several different outcomes are possible. Closing mink farms may result in a crash of the free-ranging population, or alternatively it may result in the establishment of a better adapted, truly feral population that may ultimately outnumber the population that was present before farm closures.

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Population ecology of free-ranging American mink *Mustela vison* in Denmark

This PhD thesis presents the results of various studies of free-ranging American mink *Mustela vison* in Denmark. Stable carbon isotope analyses of teeth and claws from 213 free-ranging mink from two areas of Denmark showed that nearly 80% were escaped farm mink. A genetic analysis of a sub-sample of the same animals by means of microsatellites corroborated this result. The isotope analyses permitted the separation of the mink into three groups; newly escaped mink, 'earlier' escaped mink (having lived in nature for more than ca. two months), and wild mink. The survival of these three groups differed. Once an escaped farm mink had managed to stay alive in nature for more than two months, its chances of survival were as good as for the wild mink. Mink diet consisted primarily of mammals, followed by amphibians, birds and fish. Diet of polecats from the same area is also described. Finally, the thesis gives results from model simulations (including evolution) of the possible effects on the free-ranging population of reducing the number of escapes or completely closing down fur farms in Denmark.

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